

Review of fossil crocodilians from Australasia

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ABSTRACT

Recent phylogenetic studies of fossil crocodilian material from Australia, New Guinea and New Caledonia (e.g., Willis *et al.* 1993; Willis 1995; Salisbury and Willis 1996) indicate most extinct crocodilians from Australasia form an endemic clade, the Mekosuchinae, and extant crocodilians in this region are more recent arrivals from Asia. Mekosuchines display a variety of ecomorphs in head shape ranging from small and deep to longirostrine to very deep snouted and the significance of these is discussed.

INTRODUCTION

Although fossil crocodilian material has been recovered from Australia for more than 125 years, it has only been within the last decade or so that this group has received adequate attention. This recent interest in crocodilians is the result of a dramatic increase in high-quality specimens recovered during broad-based palaeontological excavations and a consequent increase in research efforts. This group has revealed a more complicated and interesting history than previously realized. This review compiles both historic and recent literature on Australasian fossil crocodilians and attempts to summarise the current understanding of their taxonomy, phylogeny and evolutionary history.

After an opening section on the earliest literature of Australian fossil crocodiles, this paper proceeds in a broadly geochronological order looking at the known material for each taxon during each successive period. Some taxa (e.g., *Quinkana* and *Mekosuchus*) are discussed more than once because they occur in more than one geological period. Summaries of current phylogenetic analyses are then given, followed by a consideration of crocodilian evolutionary history in Australia and comment on the significance of the broad range of crocodilian ecomorphs present in Australia during the Cainozoic. Although the bulk of the crocodilians considered here are from Australia, mention is also made of fossil crocodilian material from New Guinea, New Caledonia and the Solomon Islands.

Although extensive use of unpublished work is made here, it is appropriate because it provides a more complete picture of work in this area and most of this work is nearing publication. More information of work cited in preparation can be obtained by contacting the referred researcher.

EARLY LITERATURE

The first record of a fossil crocodilian from Australia is given by Clarke (1869) who refers to

bones of crocodiles in Crinum Creek near Peak Downs in Queensland. Daintree (1872) mentions crocodile teeth from Maryvale Creek in north-eastern Queensland which he named *Crocodylus*² *australis*³. Jack and Etheridge (1892) refer all crocodile material from this site to *Crocodylus porosus*.

Typical of most British colonies of last century, important fossil specimens from Australia were sent to the major collections in England, usually the collections of the British Museum of Natural History. Thus, when Lydekker (1888) published the *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History)*, it contained the first published records of many Australian specimens and localities. Lydekker records *Crocodylus porosus* from Clifton Plains, Gowrie and the Condamine River in Queensland. These specimens were donated by Harkness in 1871, Daintree in 1872, Bennett in 1872 and Hood in 1861. Some of this material is being reassessed and may be assigned to *Pallimnarchus*.

Jack and Etheridge (1892) record a number of occurrences of crocodilian fossils in Queensland. They note the occurrences mentioned by Clark (1869), Daintree (1872) and Lydekker (1888) and list both *Crocodylus porosus* and *Pallimnarchus pollens* from the Darling Downs. In a later section of the same publication dealing specifically with the fossil vertebrates of Queensland, Jack and Etheridge list *C. porosus* from Maryvale Creek, and at Gowrie and Clifton Plains on the Darling Downs. They also list *P. pollens* from Chinchilla, Weimbilla Creek, Gowrie Creek, Condamine River and Eight-mile Plains (near Brisbane).

CRETACEOUS CROCODILIANS

There are now three published records of crocodiles from Cretaceous sediments of Australia (Fig 1). These occurrences are fragmentary and

²The archaic spelling of *Crocodylus* has been retained where employed by the authors.

³This name has also been applied to South American forms now recognized as species of *Proalligator* (Steel 1973).



Figure 1. Location of Mesozoic, early and mid Tertiary crocodile-bearing deposits in Australia. After Hills 1943; McNamara 1993; Megirian *et al.* 1991; Megirian 1994; Megirian *et al.* 1993; Molnar 1980; Molnar 1991; Murray and Megirian 1992; Murray *et al.* 1993; Rich and Rich 1989; Willis 1993; Willis 1995; Willis *et al.* 1990; Willis *et al.* 1993; Willis and Molnar 1991a; Willis and Molnar 1991b.

uninformative but probably contemporaneous and possibly conspecific. Three other, previously unpublished Cretaceous crocodilian specimens are also recorded in Australia. It is hoped that further material will be found to add to our knowledge of this important group during the Cretaceous.

Etheridge (1917) referred a small opalized fragment of reptilian mandible from Albian-Aptian deposits at Lightning Ridge, New South Wales to *Crocodylus (Bottosaurus) selaslophensis*. Molnar (1980) referred a procoelous vertebra and several other pieces from the same locality to this taxon and concluded that it represented an eusuchian.

A crocodilian quadratojugal and two scutes have been recovered from early Cretaceous sites at Dinosaur Cove, in the Otway Ranges of Victoria. This undescribed material is fragmentary and not very informative but indicates a small (under 2 m long) crocodile within the Dinosaur Cove fauna (Rich and Rich 1989).

A recent acquisition by the Australian Museum of opal fossils from Albian-Aptian deposits of Lightning Ridge, New South Wales, includes a small crocodilian dentary. This dentary is quite different from the dentary referred to *Crocodylus (Bottosaurus) selaslophensis* and is currently being studied (Willis and Molnar, in prep.). Some other crocodilian material from Lightning Ridge is also being studied by Ralph Molnar in the Queensland Museum (pers. comm.).

A posterior section of an articulated crocodilian skeleton was recovered from central Queensland in mid 1996 (Molnar and Willis 1996). This

Cenomanian specimen includes the lumbar, sacral and proximal caudal vertebrae, the pelvis and most of the hind limbs. This specimen is currently being studied by Ralph Molnar and the author.

EARLY TERTIARY CROCODILES

A number of crocodilian specimens have been recovered from Paleocene to Oligocene deposits and all come from Queensland (Fig. 1). Most of this material is fragmentary and uninformative but material from the Tingamurra deposits near Murgon and the Rundle Oil shales near Gladstone is more complete and informative. Most of this material can be referred to the genus *Kambara*.

Kambara

The early Tertiary genus *Kambara* was first described by Willis *et al.* (1993), who recognized a single species (*K. murgonensis*) from the Eocene Tingamurra deposits in south-east Queensland. Subsequently, a second species of *Kambara* has been recognized from this site (Salisbury and Willis 1996). Material from the Eocene-Oligocene oil shale deposits of Rundle, Eastern Queensland, briefly described by Hills (1943) and Molnar (1991), may represent a third, as yet undescribed species of *Kambara*. The anterior dentary from Murgon described by Molnar (1982b) has been referred to *Kambara* (Willis *et al.* 1993).

Kambara is a moderately broad-snouted, generalist crocodile notable for the disparity in size between the smallest and largest teeth (Fig. 2). This tooth disparity is also seen in other mekosuchines but *Kambara* is the earliest member of the group to display it. Distinctive sculptural patterns, such as large sculptured pits between the orbits and the supratemporal fenestrae, and a deep excavation anterior to the internal nares also characterize this genus.

A possible fourth species of *Kambara* has been recorded by Willis and Molnar (1991a) from Eocene sediments near Brisbane. This material consists of an anterior dentary fragment and an isolated vertebral centrum. This is a more longirostrine form than the other three species but it does display a similar tooth disparity.

An intriguing recent discovery is of Eocene-Oligocene crocodile scutes from Cape Hillsborough, northern Queensland (McNamara 1993). These small, squarish scutes probably belong to an advanced neosuchian but otherwise this material is uninformative.

Riek (1952) records a piece of skin and some bone fragments possibly from a crocodile found in the early Tertiary Redbank Plains Series near Brisbane. The bone fragments cannot be found

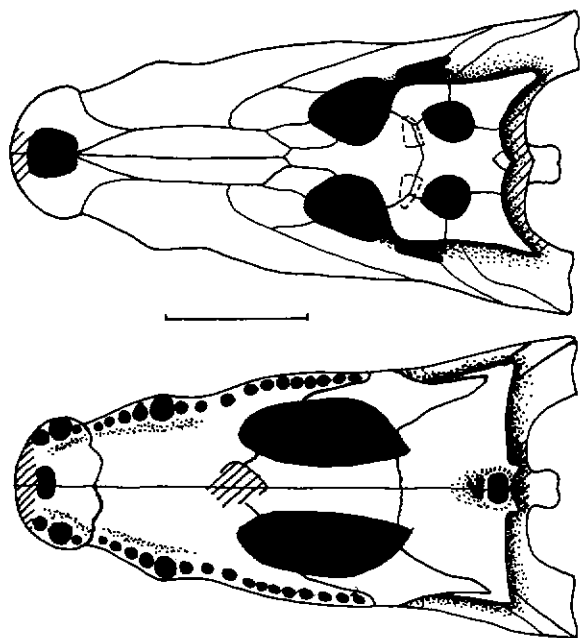


Figure 2. *Kambara murgonensis*, reconstruction of skull. Top: dorsal view. Bottom: ventral view. Scale bar represents 10 cm.

and it is not clear from Riek's paper that these fragments were actually collected. Known skin impressions from this site represent lepidosaurs and lungfish but not crocodilians (Molnar, pers. comm.).

MIDDLE TERTIARY CROCODYLIANS

Until quite recently, crocodilian material from Miocene deposits was rare and poorly understood (e.g., Woodburne 1967) but the last decade has seen a rapid increase in the number of specimens from Riversleigh in northwestern Queensland, Bullock Creek and Alcoota in the Northern Territory and Miocene deposits in the Lake Eyre Basin of South Australia (Fig. 1). Sites at Riversleigh and Bullock Creek have produced particularly diverse and interesting crocodilian faunas with some sites containing up to four crocodilian species (Willis 1992; Willis 1995; Murray and Megirian 1992).

Baru

Relatively complete cranial and mandibular material from Riversleigh and Bullock Creek formed the basis of the new genus and species *Baru darrowi* Willis *et al.* (1990). This is a moderately large (around 4 m long) crocodile with a particularly massive head, enormous caniniform teeth that are moderately compressed and a broad posterior region of the skull allowing large areas for massive jaw musculature (Fig. 3). Subsequent work has shown that the Riversleigh material represents a second species separate from *B. darrowi* of Bullock Creek (Willis 1992; Willis, in press) and that a smaller, third species also exists at Riversleigh. Species of *Baru*

are now recognized in many of the older sites at Riversleigh and the larger species is restricted to some of the very earliest sites. Similarly, another smaller species of *Baru* may be present at Bullock Creek (Willis 1995).

Crocodilian material from mid to late Miocene sediments at Alcoota was originally described by Woodburne (1967) as *Crocodylus* sp. Murray and Megirian (1992) examined new crocodilian material from the site and assigned it to a species of *Baru*, possibly *B. darrowi*. It is likely that the material Woodburne (1967) identified as *Crocodylus* actually belongs to *Baru*.

Quinkana

Species of *Quinkana* were originally recognized from Plio-Pleistocene deposits of Queensland (Molnar 1981) but recently prepared material from Riversleigh and Bullock Creek indicate new species of *Quinkana* in these earlier deposits (Willis 1992; Willis, in press; Murray and Megirian 1992; Murray *et al.* 1993; Megirian *et al.* 1993; Megirian, in prep.). The *Quinkana* species from Riversleigh are all quite small in comparison to previously known species and are distributed over a number of sites. Megirian (1994) described the new species of *Quinkana* present in Bullock Creek as *Q. timara* with a significantly narrower snout than that of *Q. fortirostrum*. The

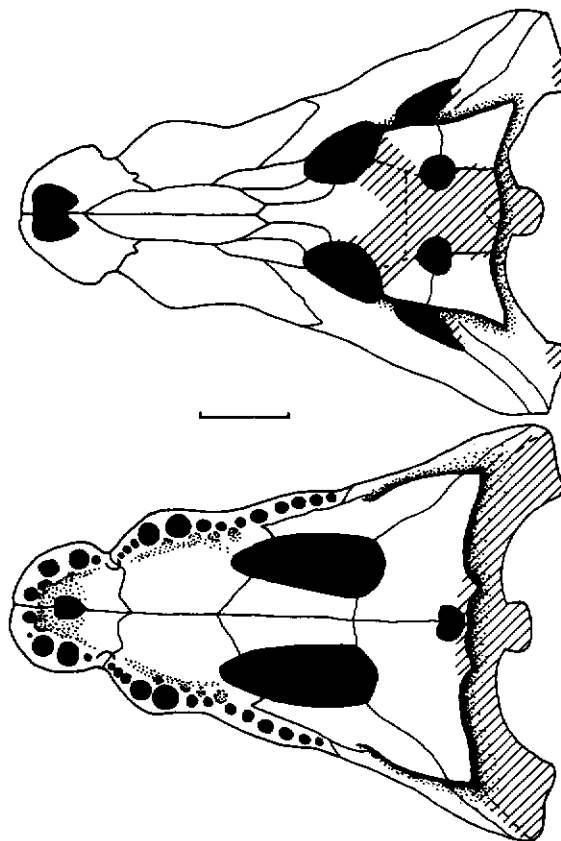


Figure 3. *Baru darrowi*, reconstruction of skull. Top: dorsal view. Bottom: ventral view. Scale bar represents 10 cm.

specific determination of the *Quinkana* in the Ongeva Local Fauna of Alcoota (Murray *et al.* 1993; Megirian *et al.* 1993) cannot be made based on material currently available.

Quinkana is a genus of ziphodont crocodilians that are demonstrably mekosuchine and endemic to Australia. Thus their acquisition of ziphodont characters is independent from and convergent on other ziphodont crocodilians from around the world. They are thought to have been fully terrestrial based on comparisons with pristichampsines and sebecosuchians and some aspects of the taphonomy of the Pleistocene species *Q. fortirostrum* (Molnar 1977; Molnar 1978a; Molnar 1978b; Molnar 1981). The early presence in Australia of ziphodont crocodilians and other large reptilian carnivores together with the absence of large mammalian carnivores indicates that the occupation of the large carnivore guild noted for Australian Pleistocene faunas (Murray 1984) probably has a much more extensive history.

Mekosuchus

A species of *Mekosuchus* was first recorded from Pleistocene or Recent deposits of New Caledonia (Balouet and Buffetaut 1987) so the appearance of two species in Miocene deposits of Riversleigh (Willis 1992; Willis 1995; Willis, in prep.) was surprising. This distinctive genus of small (less than one metre long) crocodilians is unusual in that the maxilla participates in the orbit thus excluding the lacrimal from contact with the jugal. *Mekosuchus* species have very short, deep heads and may have been terrestrial or even arboreal (see below). This conclusion is based on postcranial material from the Pleistocene species and comparison with atoposaurids, libycosuchids and notosuchids which have a similar cranial morphology.

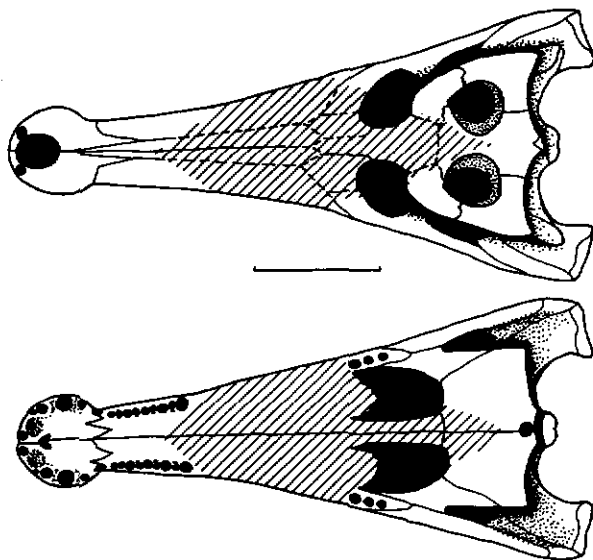


Figure 4. *Harpachampsia camfieldensis*, reconstruction of skull. Top: dorsal view. Bottom: ventral view. Scale bar represents 10 cm.

Trilophosuchus

The unusual species *Trilophosuchus rackhami* was described by Willis (1993) from Ringtail Site at Riversleigh. Similar to species of *Mekosuchus* in having a short deep head and being small, *Trilophosuchus* has the striking feature of three longitudinal crests across the skull roof. Low bumps indicate a poorly developed second pair of crests lateral to the other three. The supratemporal fenestrae are elongate and laterally compressed which is either a juvenile or paedomorphic feature. An analysis of the neck muscle insertions (Willis 1993) indicates more similarities with the morphology of the ziphodont *Pristichampsus* than to more typical, non-ziphodont crocodilians and this has been taken as tentative evidence for a terrestrial habitat for *Trilophosuchus*.

Harpacochampsia

The imperfectly known *Harpacochampsia camfieldensis* from Bullock Creek in the Northern Territory is based on a posterior cranial fragment, an anterior snout fragment and a small piece of the left dentary, all probably from the same individual, as well as some postcranial material (Fig. 4). Megirian *et al.* (1991) recognized certain longirostrine characters, such as the extremely large and cavernous supratemporal fenestrae and the globose anterior of the snout that were reminiscent of gavialids, but their phylogenetic analysis indicated mekosuchine or crocodyline affinities. More recent phylogenetic analyses (Willis 1995; Salisbury and Willis 1996) indicate that *Harpacochampsia* is likely to be a mekosuchine or crocodyloid where many key characters have been masked by the longirostrine condition. *Harpacochampsia* is a moderately large crocodilian, probably reaching lengths of 4 or 5 m and its longirostrine condition indicates a piscivorous diet.

Australosuchus

The medium sized (around 3 m in length) generalized crocodilian *Australosuchus clarkae* is known from abundant material from a number of sites in the Lake Eyre Basin, South Australia (Willis and Molnar 1991b). Being a moderately broad-snouted mekosuchine, *Australosuchus* has the unusual condition of the fourth dentary tooth notch in the snout being almost totally enclosed (Fig. 5). Complete skulls and mandibles are known of *A. clarkae* as well as abundant postcranial elements, dermal armour and an articulated partial skeleton. Reports of *A. clarkae* from younger sediments (Megirian *et al.* 1993; Willis and Molnar 1991b) are based on probably reworked specimens.

An interesting palaeobiogeographic problem is presented by the distribution of contemporaneous crocodilian taxa in Australia during the Oligo-Miocene. Although some of the sites in the Lake

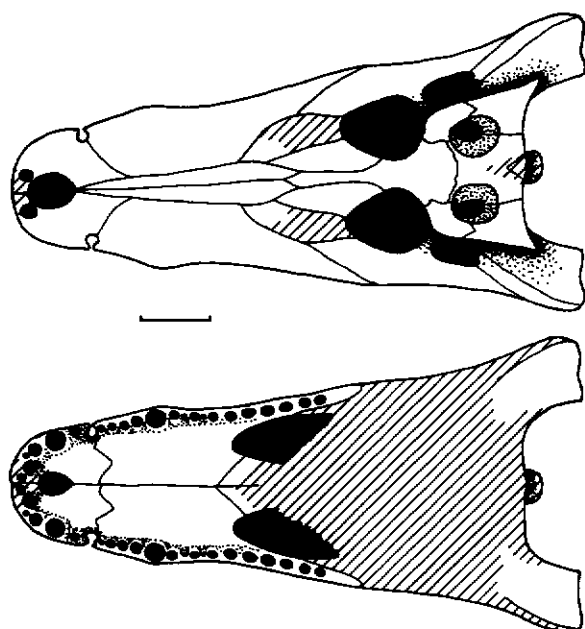


Figure 5. Reconstruction of the skull of *Australosuchus clarkae* in dorsal (top) and ventral (bottom) views. The posterior part of the cranial surface is unknown (adapted from Willis and Molnar 1991a).

Eyre Basin in South Australia and Riversleigh in Queensland are demonstrably contemporaneous (Woodburne *et al.* 1994) and there are large collections from both localities representing many crocodilian specimens, there are no common crocodilian taxa shared between the two areas. While this disparity in distribution for semi-aquatic taxa (*Baru* and *Australosuchus*) can be explained by separate and isolated drainage basins, this explanation does not extend to taxa that are supposedly terrestrial or are at least competent in terrestrial environments (*Quinkana*, *Mekosuchus* and *Trilophosuchus*). Either the barriers to distribution for small to medium sized terrestrial crocodilian taxa were formidable or their abilities to cross terrestrial environments were not as developed as has been supposed. Perhaps the "terrestrial" adaptations of *Quinkana*, *Mekosuchus* and *Trilophosuchus* represent the terrestrial limit of the operating potential of a mostly aquatic species. For example, the ziphodont characters of *Quinkana* may well have allowed it to take prey and process food on land but they were still tied to permanent water bodies for protection, reproduction or thermoregulation.

PLIO-PLEISTOCENE CROCODILIANS

The first records of crocodilians from Australia were from Plio-Pleistocene deposits of Queensland (Clarke 1869; Daintree 1872; Lydekker 1888). Subsequent excavations have revealed Plio-Pleistocene crocodilians from northern New South Wales, northern Western Australia and central South Australia (Fig. 6). Quite large crocodilians (5 m or more in length)

inhabited the inland drainage basins of Australia as well as the coastal basins until comparatively recently (late Pleistocene in most cases). The demise of crocodilians from inland Australia was probably coupled with the collapse of the megafauna and general drying out of this part of the continent.

Pallimnarchus

The first detailed discussion of crocodilian fossils from Australia was by De Vis (1886), when he named *Pallimnarchus pollens*. De Vis noted that *P. pollens* was a heavily built, large crocodilian. Later De Vis (1907) described more fossil material from the Gulf of Carpentaria and assigned this to *P. pollens*. De Vis never formally defined *Pallimnarchus* or *P. pollens* but the names gained a *de facto* validity through use in popular and scientific literature. De Vis was somewhat equivocal about the affinities of *P. pollens* variously comparing it to alligatorines and crocodylines but favouring crocodyline affinities.

Longman (1925a) described a large crocodilian snout from Lansdowne Station, central Queensland, referring it to *P. pollens*. Molnar (1982b) re-examined this specimen and identified it as *Crocodylus porosus*. Longman (1925b) also described a large, heavily built crocodilian mandible from Macalister, southeastern Queensland, referring it to *P. pollens*.

Anderson (1937) described a pair of large mandibular fragments from the Gregory River, north Queensland, referring them to *P. pollens*. There is no more precise locality information and it cannot be determined if they derived from

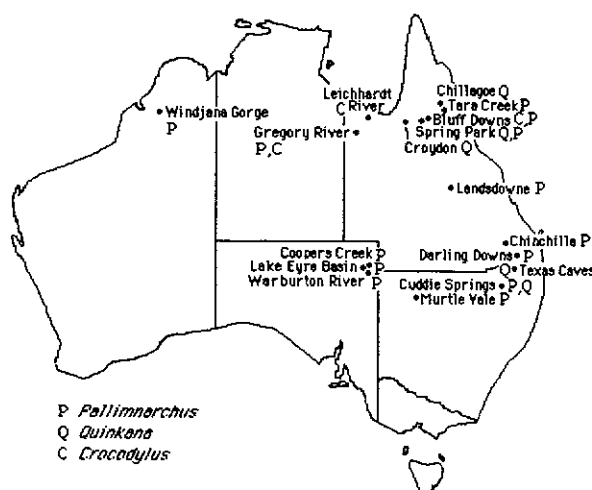


Figure 6. Location of Pliocene and Pleistocene crocodile-bearing deposits in Australia. After Anderson 1937; Anderson and Fletcher 1934; De Vis 1886; De Vis 1907; Dodson *et al.* 1993; Gorter and Nicoll 1978; Hecht and Archer 1977; Longman 1924; Longman 1925a; Longman 1925b; McNamara 1990; Megirian *et al.* 1993; Molnar 1977; Molnar 1978a; Molnar 1978b; Molnar 1979; Molnar 1981; Molnar 1982b; Tedford and Wells 1990; Thompson 1980; Willis and Archer 1990; Willis and Mackness 1996; Woodburne 1967.

Pleistocene sediments of the kind currently known from Riversleigh or some other, unknown deposit.

Molnar (1982b) reviewed the Cainozoic crocodilians of Queensland with particular attention to *Pallimnarchus*. Although the concepts *Pallimnarchus* and *P. pollens* had received widespread common usage, it was not until Molnar's revision that these concepts were properly defined and lectotype material nominated. Molnar's generic and specific definition was based on features of the anterior dentary, but referred material included other mandibular elements, premaxillae and quadrates. Molnar also described an interorbital fragment and assigned it to *P. pollens*. Molnar (1982b) showed that *C. nathani* Longman 1924 was an invalid taxon and variously assigned the *C. nathani* material to either *C. porosus* or *P. pollens*.

Willis and Molnar (in prep.) are devising a diagnostic key to aid in the identification of isolated crocodilian teeth from Plio-Pleistocene sites in Australia. The difficulty of identifying isolated teeth could mean that teeth attributed to *C. porosus* within a fauna actually represent *P. pollens*. A review of situations where misidentification is a possibility is currently being conducted. Based on isolated teeth, *Pallimnarchus* is probably present at Cuddie Springs in northern New South Wales (Anderson and Fletcher 1934; Dodson *et al.* 1993) as well as the Wyandotte Local Fauna of northern Queensland (McNamara 1990). The report of *Crocodylus* from Windjana Gorge, Western Australia (Gorter and Nicoll 1978), is based on a premaxilla and scutes and recent examination of this material by Willis and Molnar (in press) reveal that it should be referred to *Pallimnarchus*. Reports of *Pallimnarchus* from various Pliocene and Pleistocene sites in central Australia (Tedford and Wells 1990; Megirian *et al.* 1993) are based on more substantial fragments than isolated teeth.

Thompson (1980) reported two Pleistocene river bank deposits along the Darling River in western New South Wales, one of which (Myrtle Vale) contained a crocodilian tooth. Thompson describes the conical tooth as being 15 mm across the base. This could represent a large *C. porosus* but would more likely represent *Pallimnarchus* sp. because of its size. The present location of the fossils Thompson collected is unknown and the Myrtle Vale site has been submerged under the waters of a weir. Thus there appears to be little chance of correctly determining the identity of this crocodilian or of collecting more material. However, similar deposits may occur elsewhere along the Darling River (Jeannette Hope, pers. comm.). Myrtle Vale and Cuddie Springs are the most southern records of Pleistocene crocodilians in Australia.

To date only a single species of *Pallimnarchus*, *P. pollens*, has been recognised and described. However, new material and an extensive review of existing *Pallimnarchus* material reveals that a second species, and possibly more, may be represented (Willis and Molnar, in prep.).

Crocodylus porosus

Molnar (1979) identified the snout of a small crocodilian from Bluff Downs, north Queensland, reported by Archer and Wade (1976), as *Crocodylus porosus*. This is the first time fossil crocodilian material from Australia was correctly identified as belonging to this extant species. The dating of Bluff Downs is based on K/Ar dating of an overlying basalt, originally thought to be 4–4.5Ma, but recently revised to a significantly younger date within the Pliocene (Mackness, pers. comm.). This makes this specimen the second oldest fossil record of any extant species of crocodilian (the oldest being for a specimen of *Gavialis gangeticus*).

Molnar (1982b) made a case to remove the Landsdowne snout described by Longman (1925b), from *P. pollens* and place it in *Crocodylus porosus*. Recent reexamination of this specimen by Willis and Molnar (in press) reveal that it does belong to *Pallimnarchus* but probably represents a new species. Molnar (1982b) also showed that *C. nathani* was an invalid taxon and variously assigned the *C. nathani* material to either *C. porosus* or *P. pollens*. Molnar found that there was very little fossil material known from Australia that could be referred to *C. porosus*.

Crocodylus johnstoni

Being an endemic species, the apparent absence of *C. johnstoni* from fossil deposits of Australia seemed enigmatic until Willis and Archer (1990) described a dentary from Pleistocene deposits at Riversleigh, northwestern Queensland. In a note added in proof to Willis and Archer (1990), a second dentary was identified from Pleistocene deposits of Floraville Downs in northwestern Queensland. Both specimens appeared to be somewhat large for this species but they were otherwise unremarkable.

Crocodylus nathani

Longman (1924) described crocodilian material from Tara Creek, north Queensland, as *Crocodylus nathani*. He defined this taxon based on the position of the posterior extent of the mandibular symphysis and the supposed sequence of tooth enlargement that he inferred from two, unassociated mandibular fragments. This taxon is now recognized as invalid (Molnar 1982b).

***Crocodylus* sp.**

Some recent identifications of material as being *Crocodylus* sp. should, on review, be assigned to

various mekosuchine taxa. Swinton (1924) identified crocodilian remains collected from the Lake Eyre Basin, South Australia, by Gregory and referred them variously to *Crocodylus* or *C. porosus*. This material may be referred to species of *Pallimnarchus* (pers. obs.) which would be consistent with the findings of Megirian *et al.* (1993). Megirian *et al.* (1993) do record a *Crocodylus*-like specimen from the Kutjitara Formation of the Lake Eyre Basin which has possibly been reworked from other deposits. A jugal possibly referable to *Crocodylus* is also reported from the Katipiri Formation of the Lake Eyre Basin (Megirian *et al.* 1993). However, Megirian (pers. comm.) cautions that designations from these sites are based on fragmentary material with few diagnostic features.

Gorter and Nicoll (1978) referred a poorly preserved premaxillary fragment and some scutes from Winjana Gorge, Western Australia, to *Crocodylus* sp. but this material should be referred to *Pallimnarchus* (see above). Woodburne (1967) described crocodilian fossils from Alcoota, Northern Territory, and referred them to *Crocodylus* sp. but this material should probably be referred to *Baru*. Plane and Gatehouse (1967) noted the presence of "nondescript" crocodile teeth in the Awe Fauna from New Guinea. These can probably be referred to a species of *Crocodylus* but may represent a species of *Pallimnarchus*. Resolution of this matter requires a re-examination of the material.

Quinkana

The first reference to ziphodont crocodilian material from Meganesia is by Plane (1967) who recorded ziphodont teeth in the Awe Fauna from New Guinea. Hecht and Archer (1977) described two maxillary fragments, one from the Lake Eyre Basin, South Australia, the other from Texas Caves, Queensland, and referred them to an unknown sebecosuchian. Meanwhile Molnar (1977), Molnar (1978a) and Molnar (1978b), working with more complete ziphodont material from Chillagoe Caves, north Queensland, recognised that this ziphodont form was eusuchian with similarities to the pristichampsines. Molnar (1981) described and defined this form as the new genus and species *Quinkana fortirostrum* and referred to this genus the material described by Hecht and Archer (1977) from Texas Caves. Unfortunately the specimen from the Lake Eyre Basin has been lost and its referral to, or exclusion from, *Quinkana* cannot be tested. However, until evidence to the contrary can be produced, previous claims for sebecosuchians in Australia (Hecht and Archer 1977) should be discounted.

A Pliocene species of *Quinkana* has recently been recognised from the Spring Park locality, north Queensland (Willis and Mackness 1996). The new species, *Q. babarra*, differs from *Q. fortirostrum* in having a shorter snout with mild

festooning (completely suppressed in other species of *Quinkana*) and is known from a partial maxilla and isolated teeth.

Isolated ziphodont crocodilian teeth from Pleistocene localities in Meganesia should tentatively be referred to *Quinkana* sp. cf. *fortirostrum*. This includes the ziphodont teeth referred to by Plane (1967) from the Awe Fauna of Papua New Guinea, as well as teeth from Croydon, north Queensland and various sites on the Queensland Darling Downs reported by Molnar (1981) and Cuddie Springs in New South Wales as reported by Dodson *et al.* (1993).

Gavialis papuensis

De Vis (1905) described fragmentary mandibular material from Woodlark Island in the Solomon Sea as the new species *Gavialis papuensis*. Molnar (1982a) reviewed this material and assigned it to a *Euthecodon*-like crocodile. Subsequently Aoki (1988) and Molnar (1993) suggested that it could belong to a malformed individual of *Gavialis bengawanicus*. A popular account of this taxon is given by Willis (1987).

Mekosuchus inexpectatus

Balouet and Buffetaut (1987) described a small, deep-snouted crocodile from cave deposits in New Caledonia as the new genus and species *Mekosuchus inexpectatus*. These deposits were initially dated as Recent (Balouet 1991) but there is some doubt about these dates and the deposits are more likely to be Pleistocene (Tim Flannery, pers. comm.). Being an unusual, short-faced, deep-headed form, initial phylogenetic analyses erroneously suggested that *Mekosuchus* formed a sister group relationship to all other eusuchian crocodilians (Balouet and Buffetaut 1987). More recent analyses have interpreted some of the supposed symplesiomorphies of *Mekosuchus* as characters which reversed as part of a functional complex, similar to the morphology of *Osteolaemus* and *Paleosuchus* (Willis 1994, 1995).

The biogeographic distribution of species of *Mekosuchus* (Miocene species in north Queensland, Pleistocene species in New Caledonia) presents an intriguing problem. Postcranial material known for *M. inexpectatus* indicates a fully terrestrial habit. Indeed, the form of the humerus is so similar to that of species of *Varanus* it is even possible that this was an arboreal taxon. Such a terrestrial species is unlikely to have swum between Australia and New Caledonia. It is also unlikely that the distribution of *Mekosuchus* species is the result of a vicariant event, the last land bridge between the two landmasses occurred 80 million years ago in the late Cretaceous (Balouet 1991). Being a small (no more than 1 m snout-vent length) and possibly an arboreal species, the distribution of species of *Mekosuchus* may have been a dispersal by rafting from Australia to New Caledonia.

PHYLOGENETIC SYSTEMATICS

Early work on crocodilian taxa from Australia recognized various taxa as either crocodyline or alligatorine (e.g., De Vis 1886) although crocodyline affinities were favoured (e.g., Longman 1925a; Longman 1925b). *Quinkana* was initially thought to be sebecosuchian (Hecht and Archer 1977) or eusuchian, possibly pristichampsine (Molnar 1981). It was not until more recent work that similarities were recorded for Australia's endemic crocodilian taxa (Willis 1986; Willis *et al.* 1990; Willis and Molnar 1991b). Initially, this group was termed the Australian Tertiary radiation of crocodiles (Willis *et al.* 1990). Cladistic analyses supported the monophyly of these taxa (Willis 1993; Willis 1995). The subfamily Mekosuchinae was erected by Willis *et al.* (1993) to encompass the pre-existing concept of an Australian Tertiary radiation of crocodilians, redefining the taxonomic concept of Mekosuchidae originally erected by Balouet and Buffetaut (1987).

Mekosuchine characters include a great disparity of alveolar size between the smallest and largest alveoli, the development of a wedge of the supraoccipital on the dorsal surface of the skull and reduction or loss of the anterior process of the palatines. The Mekosuchinae includes *Baru*, *Quinkana*, *Mekosuchus*, *Trilophosuchus*, *Pallimnarchus*, *Kambara* and *Australosuchus*. The very derived, longirostrine genus *Harpacochampsia* (Megirian *et al.* 1991) is a problematic taxon previously of uncertain phylogenetic affinities. However, Willis (1995) presents an argument for its inclusion in the Mekosuchinae.

The Mekosuchinae forms a sister group to the Crocodylinae which includes species of *Crocodylus* and *Osteolaemus*. Character distributions are shown in Table 1 and the wider affinities of the Mekosuchinae are shown in Figure 7.

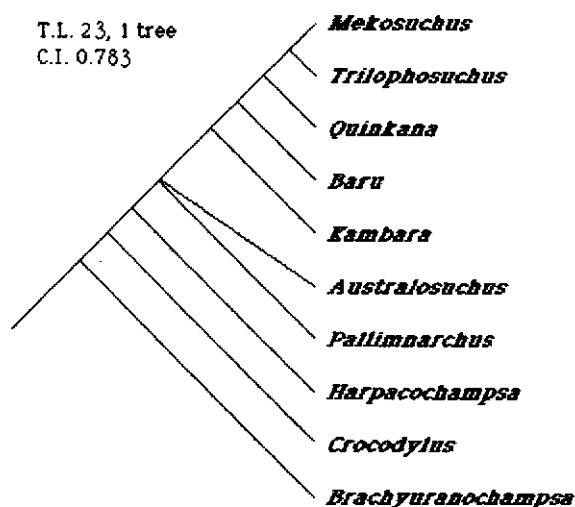


Figure 7. Cladogram showing the relationships of the mekosuchines based on an analysis of 15 characters. Characters unweighted. (After Willis 1995).

EVOLUTIONARY HISTORY

The phylogenetics of the Mekosuchinae appear to neatly fit into the zoogeographic history of Australia. The earliest representatives of the group (*Kambara* spp.) were present in Australia prior to the rifting of Australia from Antarctica and while Antarctica was still attached to South America. Such a land bridge may have offered a potential dispersal route for mekosuchines into or out of Australia. Similarly, alligatorines and other crocodilians present in South America at or prior to this time (e.g., Gasparini 1981; Gasparini 1984; Gasparini and Buffetaut 1980; Gasparini 1971; Langston 1965; Simpson 1937a; Simpson 1937b) were also presented with dispersal opportunities into Australia. However, although some mammal taxa appear to have migrated via this route (Archer *et al.* 1993, 1994), neither the mekosuchines nor South American crocodilian taxa appear to have dispersed through Antarctica.

Whatever the origin of the mekosuchines, they were present in Australia before its isolation from Antarctica and, once isolated, provided the rootstock of subsequent crocodilian faunas throughout the Tertiary until the Pliocene. Possibly as a response to the nutrient-poor environments of Australia favouring large ectothermic predators over endothermic predators (as suggested by Flannery 1994), the mekosuchines evolved diverse crocodilian faunas throughout the Tertiary including the occupation of terrestrial habitats (see below). The decline of mekosuchine diversity and their eventual extinction is probably related to the collapse of the associated Australian megafauna. Competition between mekosuchines, varanids, madtsoiids, marsupial carnivores and newly arrived crocodylines could also have contributed to the demise of mekosuchine taxa.

Two species of *Crocodylus* are currently endemic to Australia and they are not mekosuchines. The sudden appearance of the crocodylines (*Crocodylus porosus*) in the early Pliocene record of Australia (Molnar 1979) suggests a dispersal event, probably from south-east Asia, sometime in the early Pliocene or possibly the latest Miocene, as suggested by Willis (1986) and Willis *et al.* (1990). The salt tolerance of this species allows it to disperse across oceanic barriers (Taplin 1984). The subsequent appearance of *C. johnstoni* in Australia suggests a speciation from a *C. porosus* ancestor (Willis and Archer 1990).

ECOMORPHIC DIVERSITY

Mekosuchines display a broad range of ecomorphs from small taxa such as *Mekosuchus* and *Trilophosuchus* (probably less than 1 m long) to comparative giants such as *Pallimnarchus* (reaching lengths in excess of 5 metres). Even more striking are the differences in head shape from small deep "box-heads" (*Mekosuchus* spp.

Table 1. Character distribution for analysis of the Mekosucharine.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Number of unknowns
<i>Mekosuchus</i>	1	2	1	1	1	1	2	1	1	?	1	0	1	1	0	1
<i>Trilophosuchus</i>	0	1	?	1	1	?	2	1	1	?	1	0	2	1	0	3
<i>Quinkana</i>	1	2	1	0	?	1	2	1	1	1	1	1	?	0	?	3
<i>Baru</i>	1	2	1	1	?	1	1	1	1	1	0	1	0	0	1	1
<i>Kambara</i>	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1
<i>Australosuchus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Pallimnarchus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0
<i>Harpacochampsa</i>	?	1	1	1	0	0	0	?	0	0	0	0	0	0	0	2
<i>Crocodylus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Brachyuranochampsa</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknowns	1	0	1	0	2	1	0	1	0	2	0	0	1	0	1	

Character states

- (1) Presence or absence of an anterior process of the palatines.
Present (0)
Absent (1)

(2) Presence or absence of an alveolar process.
Absent (0)
Low alveolar process (1)
Well developed alveolar process (2)

(3) Size of the fifth premaxillary alveolus relative to the first maxillary alveolus.
Fifth premaxillary tooth smaller than the first maxillary tooth (0)
Fifth premaxillary tooth larger than the first maxillary tooth (1)

(4) Presence or absence of a great disparity in tooth size.
Small tooth disparity (0)
Large tooth disparity (1)

(5) Presence or absence of a supraoccipital wedge.
Absent (0)
Present (1)

(6) Shape of the external nares.
Oval or round nares (0)
Trapezoidal nares (1)

(7) Depth of the snout.
Shallow snout (0)
Moderately deep snout (1)
Very deep snout (2)

(8) Location of the palatal fenestrae.
Posterior to 8th alveoli (0)
Reach or anterior to the 8th alveoli (1)
- (9) Location of the orbits.
Posteriorly located orbits (0)
Anteriorly located orbits (1)

(10) Form of the snout notch.
Symmetrical notch (0)
Inclined notch (1)

(11) Direction of the orbits.
Dorsally facing orbits (0)
Laterally facing orbits (1)

(12) Degree of alveolar compression.
Rounded section (0)
Compressed section (1)

(13) Degree of lateral compression of the supratemporal fenestrae.
Uncompressed supratemporal fenestrae (0)
Moderately compressed (1)
Strongly compressed (2)

(14) Degree of participation of the pterygoids in the narial passage.
Restricted pterygoid participation (0)
Extensive participation (1)

(15) Size of the supratemporal fenestrae.
Moderate sized supratemporal fenestrae (0)
Small fenestrae (1)

and *Trilophosuchus rackhami*), to long but broad-snouted ziphodonts (*Quinkana* spp.), to massive-headed, "hatchet-mouthed" taxa (*Baru* spp.), to moderately broad snouted, generalized forms (*Australosuchus clarkae* and *Kambara* spp.) to large, very broad snouts (*Pallimnarchus* spp.) and the longirostrine condition (*Harpacochampsa camfieldensis*). Meyer (1984) demonstrated that more than one species of crocodilian can live sympatrically if they have different head shapes. The difference in head shape reflects differing diets and thus resources can be divided by sympatric species. This rule holds true for most Australian localities where more than one species of crocodile has been found. For example in Bullock Creek there is a large species of *Baru* and possibly a second, smaller species, a ziphodont species of *Quinkana* and a longirostrine species of *Harpacochampsa*. More difficult to explain is Ringtail Site at Riversleigh which has a species of *Mekosuchus* and *Trilophosuchus rackhami*. Both

these species are similar in size and aspects of their cranial morphology. Either the differences in skull morphology that exist between these two species reflect enough diversity of resource use to allow the two to be sympatric or the two species are found together only in a death assemblage and were not sympatric in life. The recognition of a second species of *Kambara* in the deposits of Murgon, identical in size to *K. murgonenses* and with a very similar skull morphology, raises a similar problem.

CONCLUSIONS

Despite a large collection of fossil crocodile material having been compiled from all over Australia and Meganesia prior to the 1980s, this material received little attention. As a consequence the history of crocodilians in this area was poorly understood. A dramatic increase in the amount and quality of material that became available during the 1980s and the

consequent increase in interest in this group has provided a more complete understanding of crocodilians in Australia and has produced some interesting and unexpected results. There is no reason to suggest that ongoing research on fossil crocodilians from Australia will not continue to be productive. Of particular interest is the origin of the mekosuchines and their associated dispersal into Australia. On-going research into the fossil crocodilians of Australia is being conducted by myself and Steve Salisbury at the University of New South Wales, Ralph Molnar at the Queensland Museum, Dirk Megirian at the Northern Territory Museum of Arts and Sciences and Neville Pledge of the South Australian Museum.

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BOOK REVIEWS — BOOK REVIEWS

From Coastal Wilderness to Fruited Plain: a history of environmental change in temperate North America, 1500 to the present by G. G. Whitney (1994). Cambridge University Press. ISBN 0-521-39452-X \$145.

The study of environmental history has achieved popularity in the last few decades. At least three reasons can be advanced for the development of this new discipline — that it is fascinating in its own right, that by understanding the past we may also understand the present, and that we might learn from the past in order to better plan for the future (although there is little evidence from any field of human endeavour that those who know about the past have much influence on those who do not).

Whitney's book is a very handsome and readable work. Given its price, it is unlikely that many individuals will buy it and libraries may well need considerable persuasion before adding it to collections. Other than the general interest in environmental history, are there reasons why Australian readers should be encouraged to exercise their persuasive skills on librarians? I would argue that there are.

The title of the book is somewhat misleading. Temperate North America is interpreted as eastern United States, with only the briefest mentions of Canada and western US. Although there are useful if brief discussions of grasslands and wetlands, the book is primarily an environmental history of forest, and particularly forest clearance. Although the concerns of early conservationists are discussed, the development of a reserve system and its influence on land use is not discussed, nor is the growth of legislation and regulation designed to influence conservation and land use planning explored.

Nevertheless, there is much in the book of interest to a student of Australian environmental history. The two countries have similar histories of European

colonization and resource exploitation. What is strikingly different is the time scale. The process of clearing and developing the Europeanized American landscape is spread over nearly five hundred years; in Australia the European impact has taken only two hundred years. Given that the European population in North America was much greater than that in Australia one could almost accuse our American cousins of being wimps! A feature of the American experience is that substantial cleared areas have subsequently reverted to forest (indeed the study of the old field succession has been a major topic in American ecology); to date, at least, reversion on a comparable scale has not occurred in Australia.

Whitney discusses at length the three major exploitative uses: clearing for agriculture, the development of forestry, and the use of wood as a fuel. Despite utilization of resources for several centuries it is clearly demonstrated that the greatest assault on the eastern forests, both for timber and fuel, was in the half century after 1850. The impact of exploitation on the environment is carefully evaluated. In Australia one of the early themes in the exploitation of forests was the search for cedar, and the cedar getters played an important role in exploration and resource assessment. It is striking that a similar tale can be told for the forests of eastern America, only here the search was for White Pine *Pinus strobus*, especially valued for ships' masts.

Whitney also documents the exploitation of native fauna and the impacts of clearance of forests on wildlife. One useful piece of trivia to be gained from this discussion is that deer skins were considered an item of commerce and that the term "buck" for dollar derives from the equivalence of a buckskin with a Spanish dollar.

A useful early chapter discusses critically the data sources available for constructing environmental